SPORES, CHROMOSOMES AND RELATIONS OF THE FERN PELLAEA ATROPURPUREA

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The Purple Cliff-Brake, *Pellaea atropurpurea,* is the only American species of the large complex of cheilanthoid ferns that has a range extending from the tropics into northern regions, including New England. Only triploid plants are known, which evidently are hybrids, and they are apogamous with 87 chromosomes in the sporophyte and spore mother cells. The species is a tool of some biological interest as there appears to be no evidence of sexual reproduction, although the specimens are highly variable throughout the geographic range. Northern Mexico and the adjacent southwestern United States is regarded as a center of dispersal of *Pellaea* section *Pellaea* in America, for eleven of the fourteen species have distributions that converge there or have close relatives that do. Studies of the cytology and spores of *P. atropurpurea* and two other species, *P. notabilis* and *P. ternifolia,* that occur in this central area, provide new data for establishing relationships among these species, and insights on the possible origin of *P. atropurpurea.*

MATERIAL AND METHODS

The general geographic distributions of the taxa are outlined on the maps; localities more than 600 miles from the main range are indicated by separate dots. Ranges are based on data from my revision of *Pellaea* section *Pellaea* (A. Tryon, 1957) and from recent reports of range extensions. The wide cytological sampling of populations is shown on the maps. The new cytological records are combined with earlier ones in Table 1. Meiosis was studied in sporangia fixed in 3:1 absolute ethyl alcohol: glacial acetic acid. Mitosis was examined in root tips fixed in the same solution following pretreatment for three hours with saturated aqueous solution of paradichlorobenzine.

Scanning electron microscope photographs were obtained from spores undercoated with carbon prior to coating with an alloy of palladium-gold while rotating and tilting the

TABLE 1. CHROMOSOME NUMBERS OF PELLAEA (*previous report, see text).

Species	Number	Ploidy	Collector	Locality
Pellaea atropurpurea	87-meiotic	3×	*Tryon & Tryon* 5523 (MO)	USA: Mo., Gray Summit *
	87-meiotic	3×	*T. Taylor*, in 1951 (UBC)	Canada: B. C., Fairmount Hotsprings *
	87-meiotic	3×	*Monette*, in 1950 (DOA)	Canada: Que., Campbell's Bay *
(Figs. 9, 16)	87-meiotic	3×	*Rollins & Tryon* 5860 (GH)	Mexico: N. L., Chipinque Mesa
(Fig. 11)	87-meiotic	3×	*Rollins & Tryon* 5860 (GH)	Mexico: N. L., Chipinque Mesa
Pellaea notabilis	29	2×	*Knobloch* 1963 (GH)	Mexico: N. L., C. San Francisco
(Figs. 12, 15)	29	2×	*Marroquin* 1855 (GH)	Mexico: N. L., C. San Francisco
Pellaea ternifolia	29	2×	*Tryon & Tryon* 5105 (MO)	Mexico: Mor., Cuernavaca *
var. *ternifolia*	29	2×	*Rollins & Tryon* 58219 (GH)	Mexico: S. L. P., San Miguelito
(Figs. 13, 17)	29	2×	*Riba* 408 (GH)	Mexico: Pueb., Hac. Batán
	58	4×	*Tryon & Tryon* 5105 (MO)	Mexico: Mex., Valle de Bravo *
	58	4×	*Rollins & Tryon* 58218 (GH)	Mexico: S. L. P., San Miguelito
Figs. 14, 18)	58	4×	*Riba* 412 (MEXU)	Mexico: Pueb., Hac. Batán
Pellaea ternifolia	87-meiotic	3×	*Knobloch* 1624 (MSC)	USA: Ariz., Sa. Catalina mts. *
var. *Wrightiana*	87-meiotic	3×	*Knobloch* 1624 (MSC)	USA: Ariz., Sa. Catalina mts. *
	58	4×	*Wagner* 64006 (MICH)	USA: N. C., Alexander Co. *
	58	4×	*Cobean* sn. (UC)	USA: N. M , Whites City *

sample. The original magnifications of the photographs of whole spores were taken at 1000 × and portions in greater detail at 5000 ×. Spore measurements are of the greatest diameter of spores in lactic acid, including the outer perine layers. Range and mean measurements are based on samples of 100 spores — 25 from each of four collections — except for *Pellaea notabilis*, in which 50 spores were measured from each of two collections.

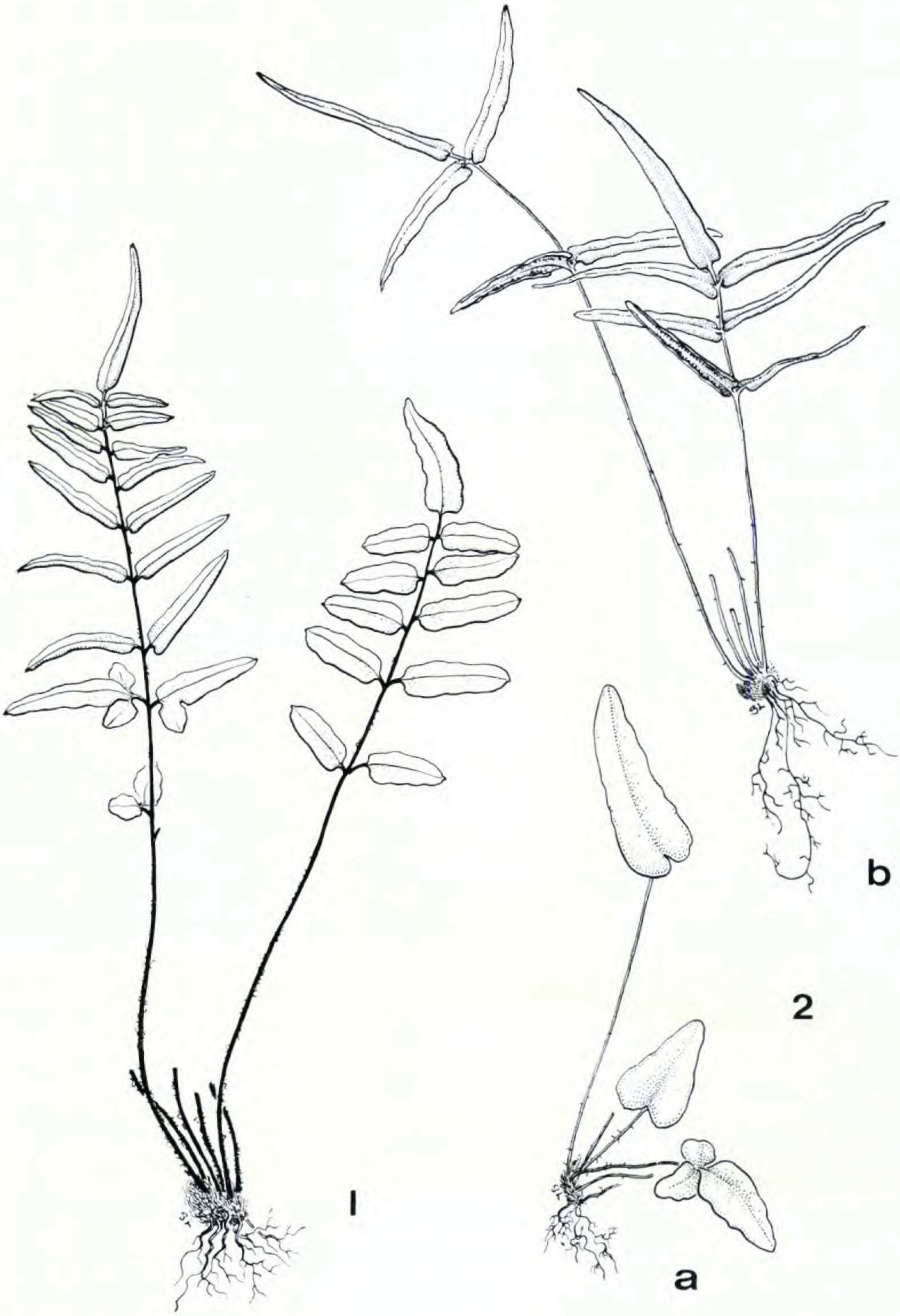
Measurements of the pinnae are of the longest fertile pinnae in the central portion of the lamina. Data are drawn from the revisionary study cited and additional specimens in collections of the Gray Herbarium, the Field Museum of Natural History, and the Smithsonian Institution.

ACKNOWLEDGMENTS

I am most appreciative of the help of Drs. Donald M. Britton and Rolla Tryon for reading and helpful comments on the manuscript. I am also grateful to Dr. Robert H. Mohlenbrock for the use of the Cambridge Stereoscan scanning electron microscope, at the University of Southern Illinois, Carbondale and the assistance there of Judith Murphy with Figs. 31-33. Other spores were examined with an AMR instrument model 900, Harvard University; the help of G. R. Pierce in the McKay Laboratory is much appreciated. Drawings of the habit and leaf detail were done mostly by Sarah Babb Landry but also by Mary Robbins.

GEOGRAPHY AND ECOLOGY

The leaves of *Pellaea atropurpurea* (L.) Link are dimorphic, and several specimens from Mexico have leaves with mostly simple pinnae as in Fig. 1. The species ranges from Guatemala northward along the Sierra Oriental of Mexico, northeast across the United States to Vermont, southern Quebec and Ontario, and there are disjunct records from areas in southern British Columbia and Alberta and also north of Lake Athabaska, Saskatchewan (Fig. 3). It occurs on exposed or shaded ledges and in crevices of limestone cliffs, on talus slopes, masonry walls,



Figs. 1, 2. Habit of *Pellaea:* Fig. 1. *P. atropurpurea* with leaves of most simple form, Puebla, *Arsène* 3548 (GH); Fig. 2. *P. notabilis* with dimorphic leaves, Nuevo Leon, *Knobloch* 1963, (GH), a. Young plant, b, Fertile leaves on mature plant; both from spores. All × ½.

or in rocky loam in woods, at 300-3200 meters. At its southernmost station in Guatemala it grows in crevices of ancient Indian pyramids. At Campbell's Bay, in Quebec, near Ottawa, it occurs on precambrian rocks in which limestone is incorporated. In Ontario it is reported by Rigby (1968) to occur in sheltered locations on talus or limestone paving, rather than exposed cliffs.

Leaves of mature plants of *Pellaea notabilis* Maxon are usually dimorphic and the pinnae simple. The first leaves are entire and cordate, and the older ones rarely have a compound lamina as in Fig. 2. Collections are known from the vicinity of Victoria, Tamaulipas, at 320 m. and from Nuevo Leon (Fig. 3). In the latter state it grows on calcareous rocks at 1100 m. in San Francisco canyon, south of Monterrey, and *P. atropurpurea* has also been collected there. Plants of *P. notabilis,* grown from spores of two collections from this canyon, produced fertile leaves in six months. The rapid and vigorous growth of these plants in culture suggests that some external factors are responsible for the limited distribution of the species.

Pellaea ternifolia (Cav.) Link car. *ternifolia* is the widest ranging of all the American pellaeas occurring from southern Texas to Argentina and Hawaii, at 200-4000 m. Both diploids and tetraploids (Figs. 5, 6) are known in the variety, and both occur at the same localities in the states of Durango and Michoacán as well as the stations reported here. Ecological data from these collections as well as field observations show that the tetraploids grow in more shaded, wetter sites than the diploids. The localities for the three cytologically documented plants are shown on the map of the general range of the variety in continental North America (Fig. 7). In addition to these tetraploids other specimens which are morphologically similar, including those reported by Pray (1967) from Mexico and Texas, are included on the map.

The leaves of *Pellaea ternifolia* var. *Wrightiana* (Hook.) A. Tryon (Fig. 4) most closely resemble the form of the diploids in var. *ternifolia,* and variation in these is noted

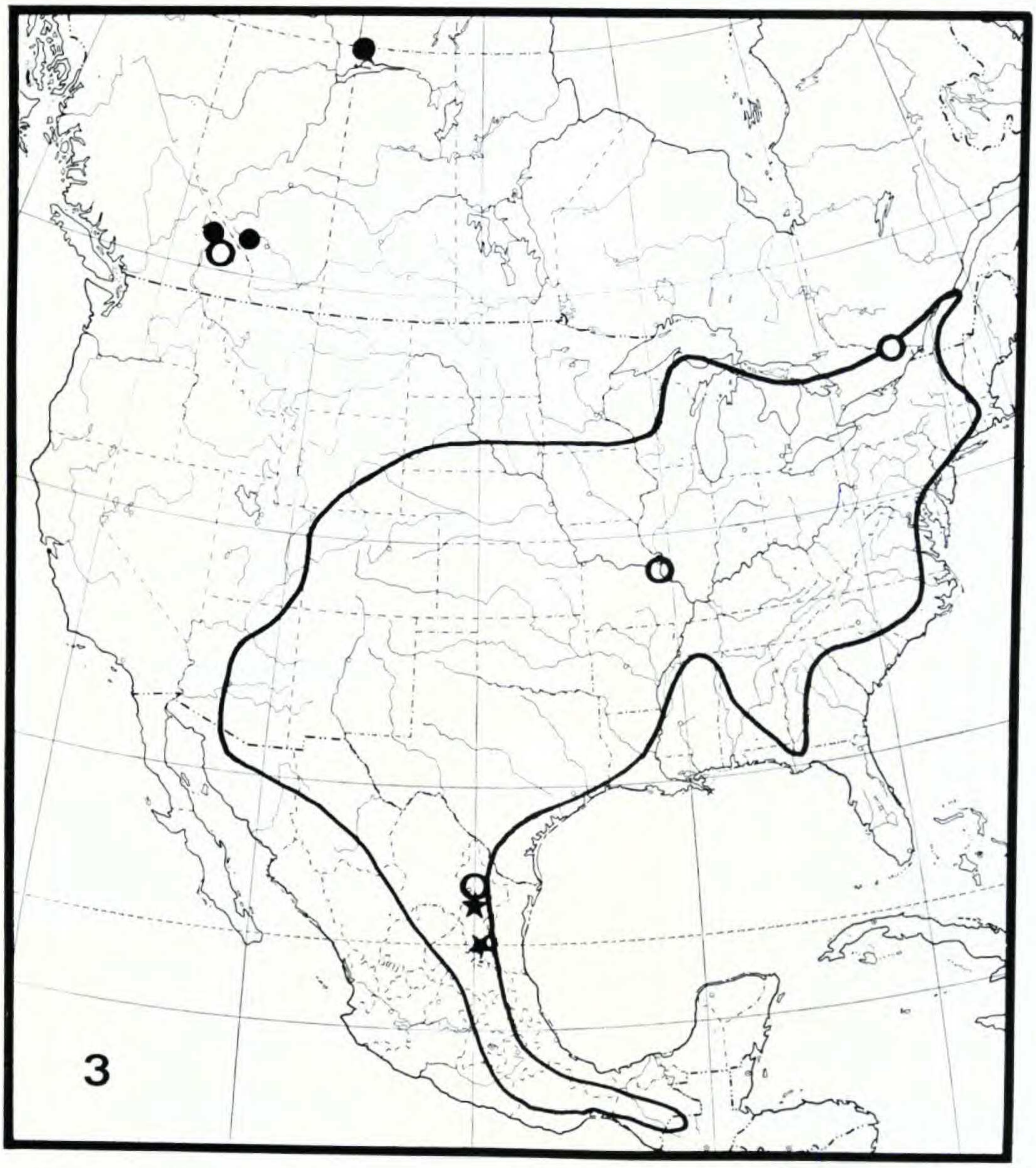
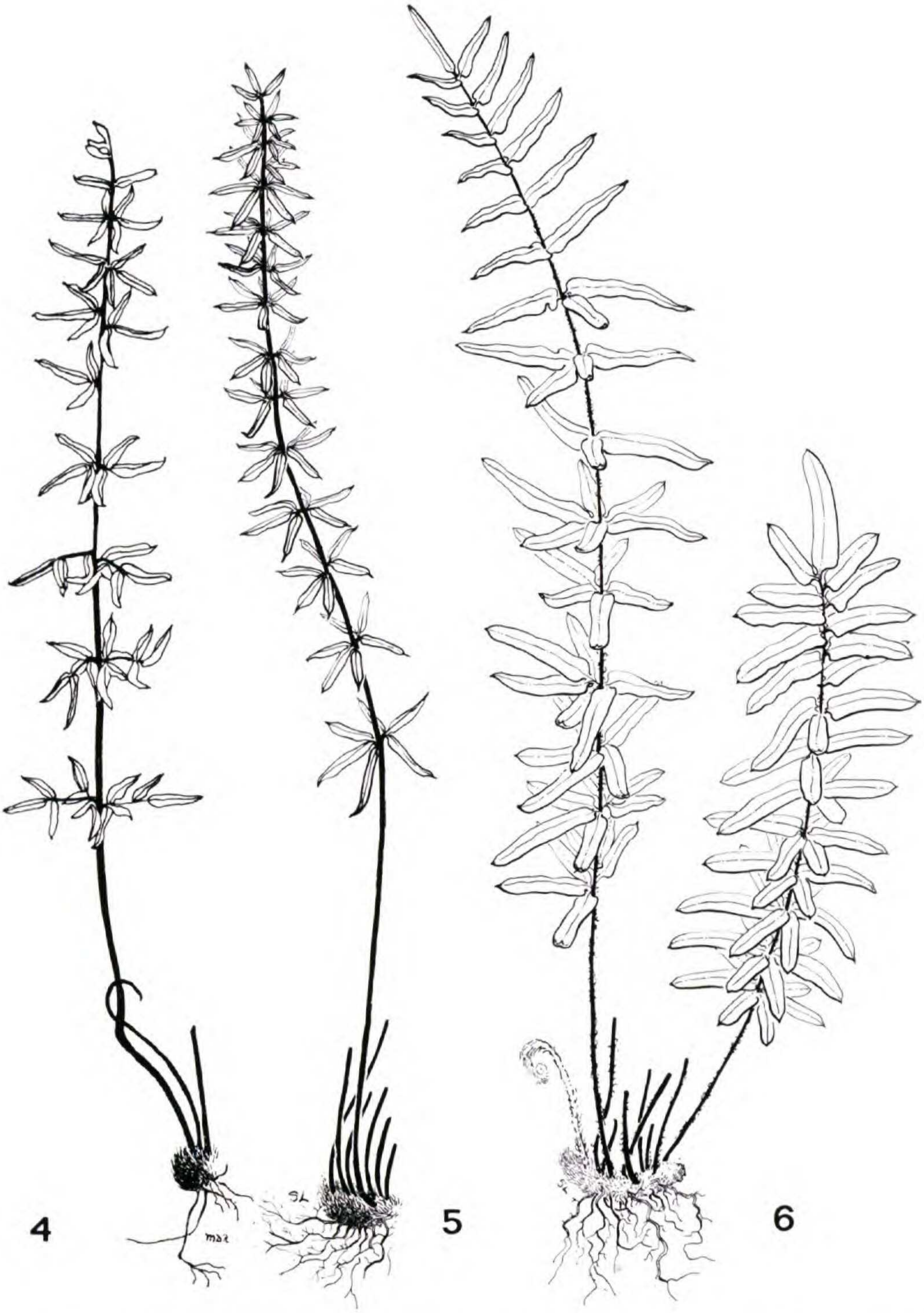
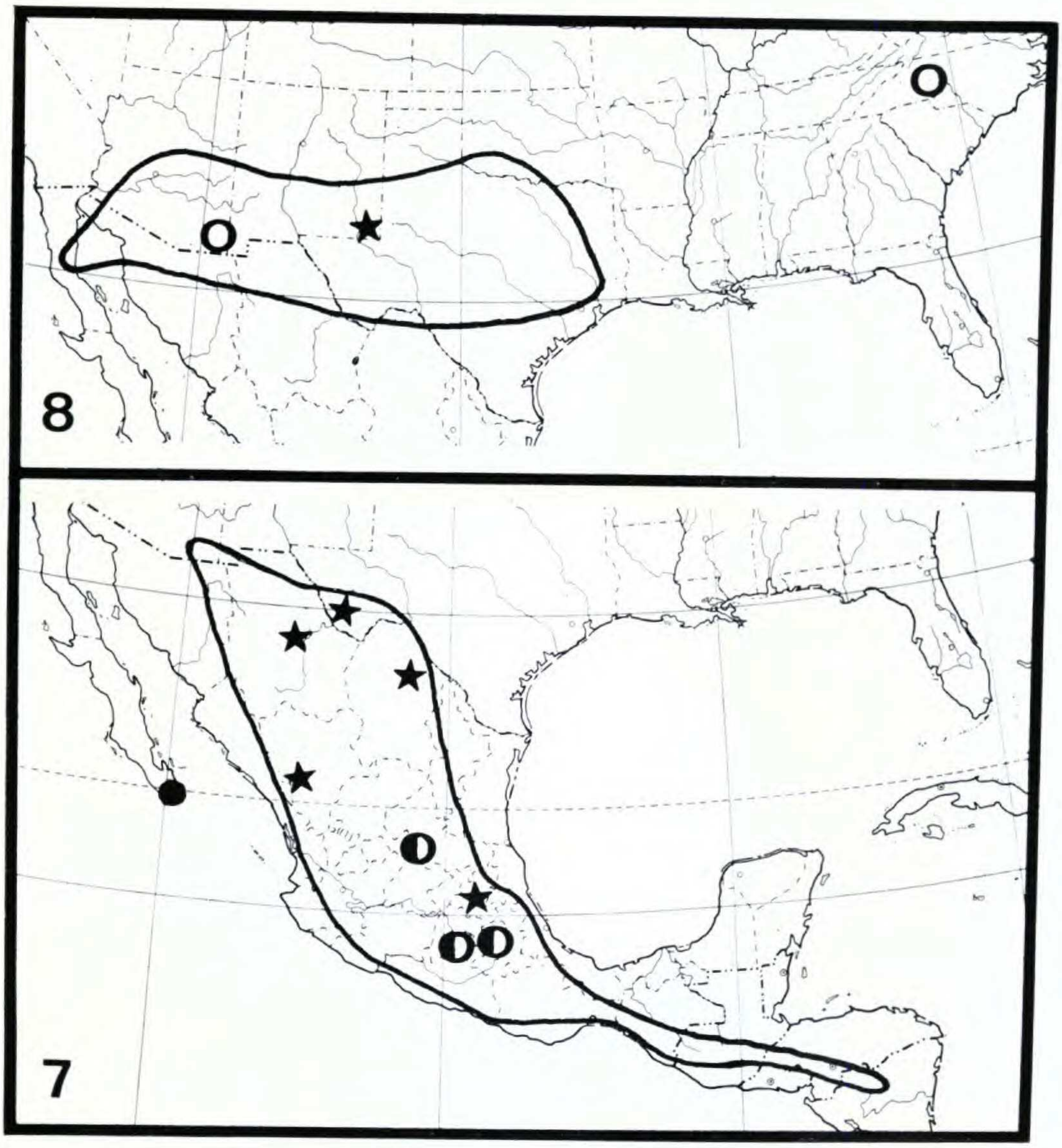


Fig. 3. *Pellaea atropurpurea* and *P. notalilis: P. atropurpurea* outlined dots-disjunct stations, circles-cytological records; *P. notabilis* stars-the upper a cytological record.



Figs. 4-6. Habit of *Pellaea ternifolia:* Fig. 4. var. *Wrightiana*, Burro mts., New Mexico, *Rusby* in 1880 (GH); Figs. 5, 6. var. *ternifolia:* Fig. 5. Diploid, Puebla, *Riba* 408 (GH). Fig. 6. Tetraploid from culture, San Luis Potosí, *Rollins & Tryon* 58218 (GH). All × ½.

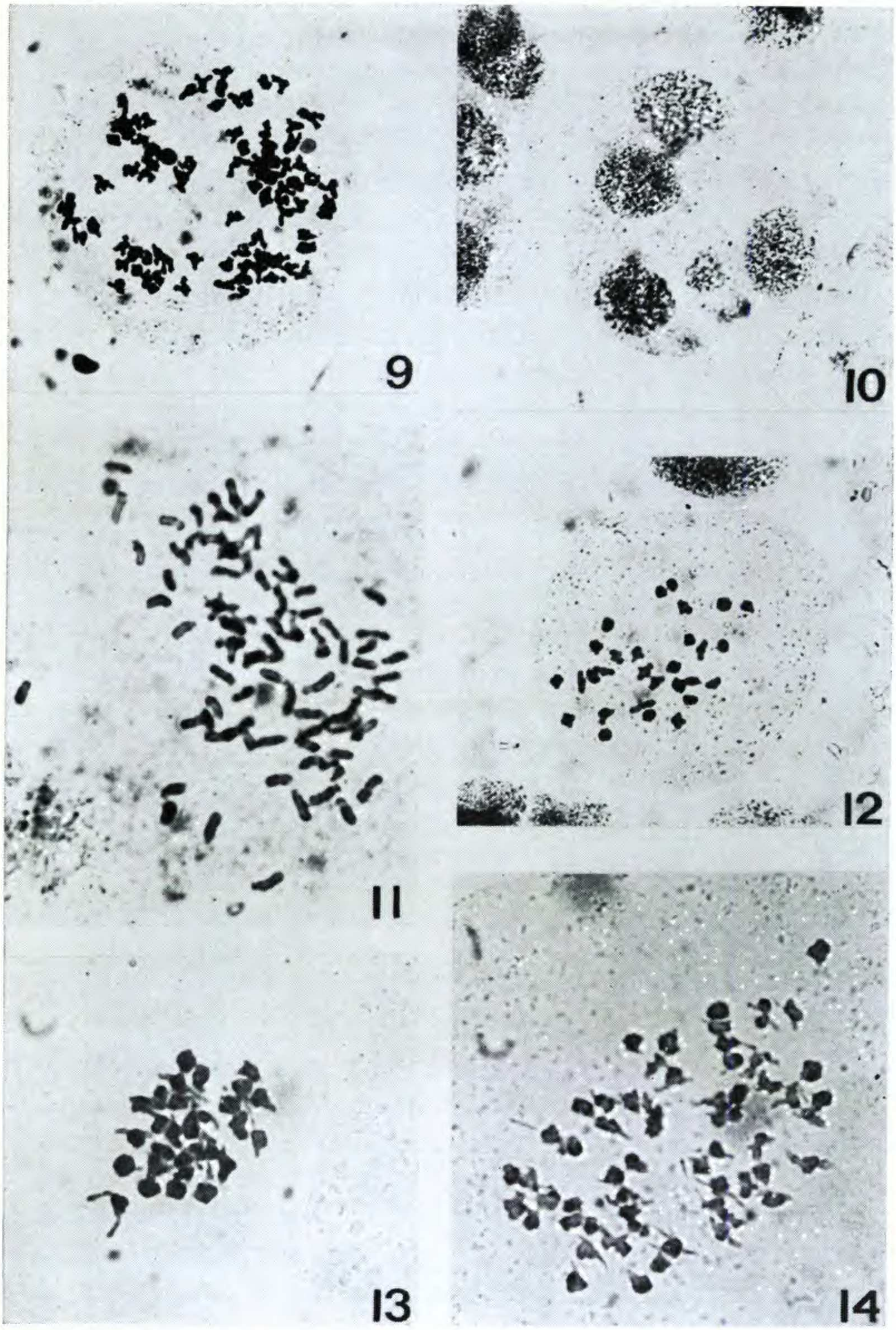


Figs. 7, 8. Range of *Pellaea ternifolia:* Fig. 7. var. *ternifolia* outlined, dot-disjunct station, stars and circles-tetraploids, circles-cytological records, half circles-localities of both diploids and tetraploids; Fig. 8. var. *Wrightiana*, circles-tetraploids, star-triploid.

in the section under morphology. The geographic range of var. *Wrightiana* extends from southern Oklahoma southwest to Arizona and across the Mexican border in northern Chihuahua, Coahuila and Baja California, at 1400-2300 m. (Fig. 8). A disjunct station is also reported about 1000 miles eastward in Alexander Co. in western North Carolina. This latter record may indicate a formerly more continuous distribution of these plants across the southern United States similar to the present range of *P. atropurpurea*, or possibly long distance dispersal from populations farther west. Specimens are mostly from exposed situations, among sandstone or granitic rocks or rarely on limestone. A few collections of somewhat larger specimens are from shade, in moist forested sites.

CYTOLOGY

Mitosis and meiosis were examined in plants of *Pellaea atropurpurea* from Chipinque Mesa, south of Monterrey, Mexico. In the mitotic cells many chromosomes have subterminal centromeres as shown in Fig. 11. Differences in the position of centromeres, in chromosome size, and the occurrence of satellites, are diagnostic aspects useful in karyotype analyses. In these apogamous plants most sporangia have eight spore-mother-cells, and some sixteen-celled sporangia are also formed. In meiotic nuclei, the nucleoli are conspicuous and persist through diakensis. Their structure can be distinguished from the bivalents in Fig. 9 by the circular form and lighter stain. In the eight-celled sporangia the chromosomes are usually associated in bivalents (Figs. 9, 16), and this is also reported by Manton (1950) and Rigby (1968). In apogamous plants the chromosome number in sporangia with eight spore-mother-cells, according to Manton, undergoes premeiotic doubling to accommodate reduction. In sixteen-celled sporangia, at meiosis, Manton (1950) and Britton (in Tryon & Britton, 1958) report approximately 29 pairs and 29 single chromosomes. The pairing associations in several cells from both types of sporangia were studied by Rigby. In these, two cells from sixteen-celled sporangia (a specimen from Que-

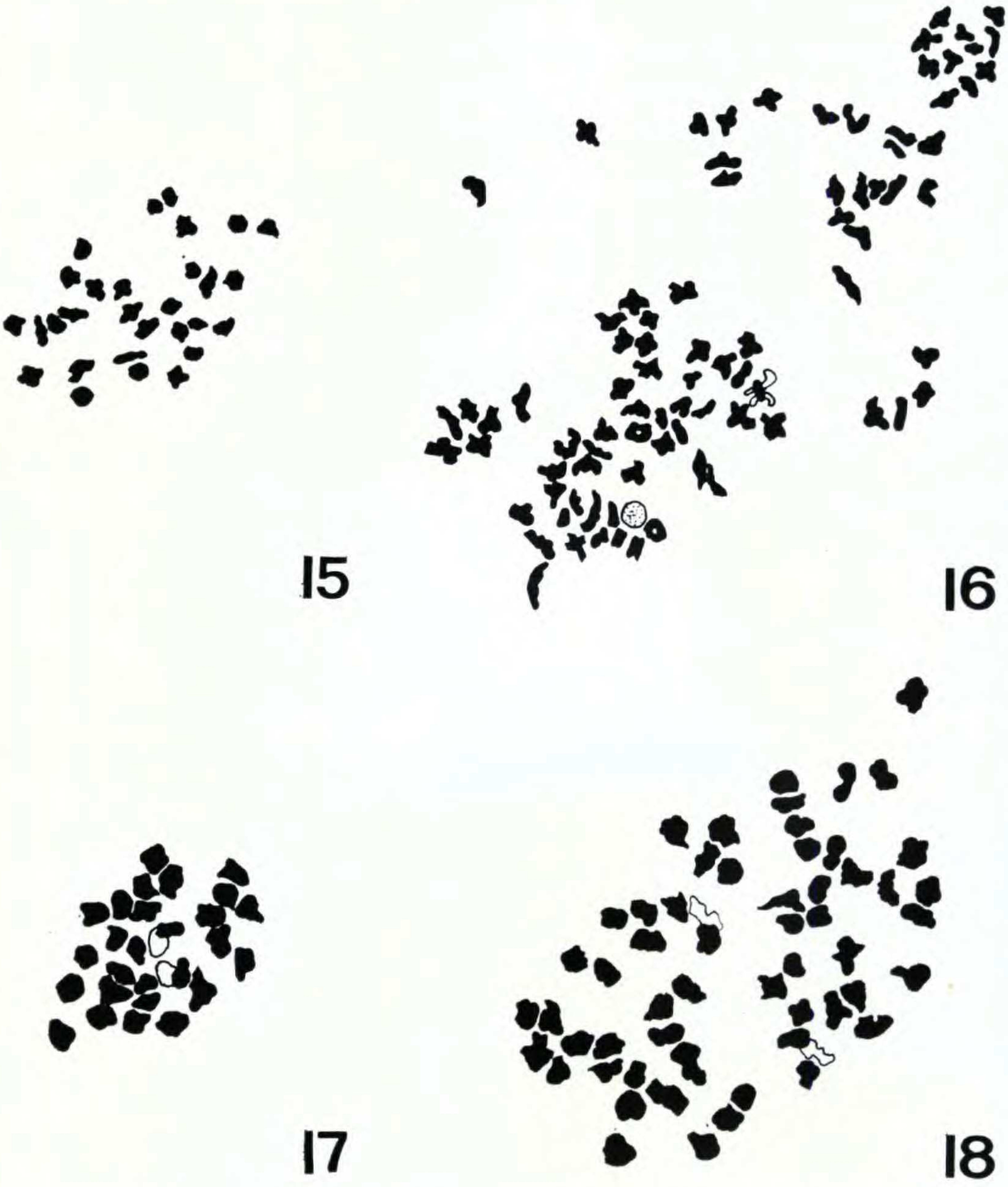


Figs. 9-14. Meiotic and mitotic nuclei: Figs. 9-11. *Pellaea atropurpurea:* Fig. 9. Nucleus from 8 celled sporangium with 87 bivalents, the nucleolus at upper right, × 660; Fig. 10. Early stage in sporogenesis, micronucleus and 4 nuclei at center, × 600; Fig. 11. Mitotic chromosomes from young sporangium. All triploid, $n=87$, *Rollins & Tryon* 5860 (GH). Fig. 12. Meiosis, *P. notabilis*, diploid, $n=29$ Marroquin 1855 (GH) × 660. Figs. 13, 14. Meiosis, *P. ternifolia* var. *ternifolia:* Fig. 13. Diploid *P. ternifolia* var. *ternifolia;* Fig. 13. Diploid, $n=29$, *Riba* 408 (GH) × 1000; Fig. 14. Tetraploid, $n=58$, *Riba* 412 (MEXU) × 1000.

bec) had equal numbers of pairs and univalents, but one had nine and the other six trivalents. A second collection (from British Columbia) had 31 bivalents, 22 univalents and one trivalent. Affinities between the parental genomes are expressed in these cells by the associations of more than 29 bivalents and also the trivalent formations. The variations in chromosome associations in these cells and also the lack of multivalents in the eight-celled sporangia, which have doubled the chromosome number, raise problems in the interpretation of chromosome pairing in these plants. There are frequent irregularities as shown in the early stage of sporogenesis in Fig. 10, in the sixteen celled sporangia, with an extra micronucleus.

Two collections of *Pellaea notabilis* from Nuevo Leon uniformly had 29 bivalents at meiosis as in Figs. 12, and 15. This establishes the species as a diploid with the basic chromosome number for *Pellaea*. The number is consistent with the species being proposed as one of the elements involved in the origin of the triploid *P. atropurpurea*.

Both diploid and tetraploid plants of *Pellaea ternifolia* var. *ternifolia* were studied from the same localities near San Luis Potosi and also farther south near Puebla. There are earlier records of these two polyploid levels, reported by Britton, from localities near Mexico City but not at the same site. The diploid with 29 bivalents and the tetraploid with 58, in Figs. 17, 18 are collections from Puebla. Contrast in the number of bivalents at late metaphase in these two polyploid levels is readily apparent in the figures. The terminal portions of the chromosomes in the centromeric regions in Figs. 13, 14 are stretched thinner than the remainder of the chromosomes forming the bivalents. These attenuated portions show tension on the late metaphase chromosomes as they prepare to move to the poles. The tetraploid plants generally resemble the diploids, but the pinnae tend to be entire and the rachises more pubescent (Figs. 5, 6) as compared to the diploids, which have ternate pinnae and nearly glabrous leaves. The drawing of the tetraploid in Fig. 6 represents an especially robust plant



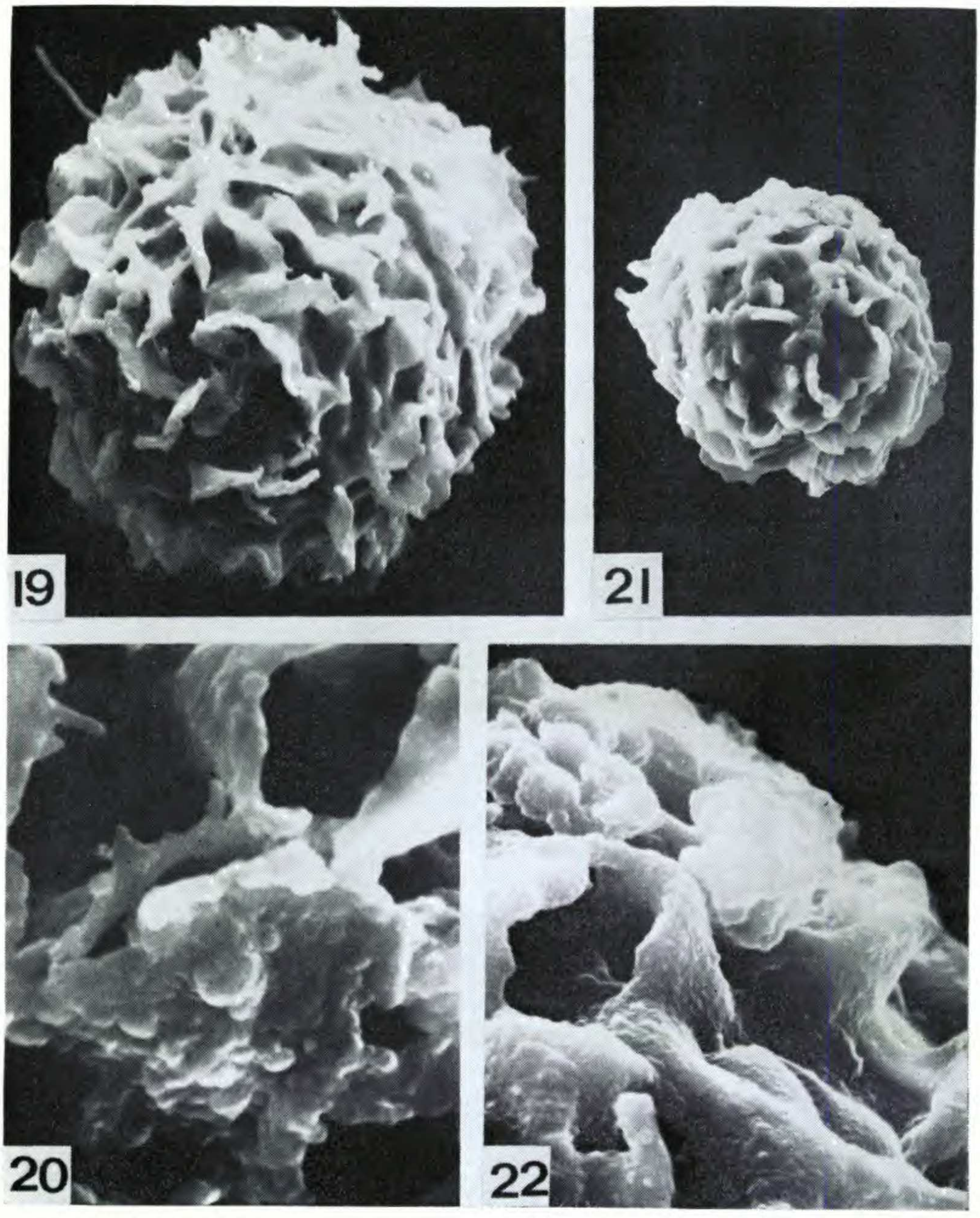
Figs. 15-18. Explanatory diagrams of meiotic nuclei (Figs. 9-14) showing bivalents in focus in black, others in outline, nucleolus stippled, from the same cells except *P. atropurpurea:* Fig. 15. *P. notabilis,* Fig. 16. *P. atropurpurea,* $n=87$, *Rollins & Tryon* 5860 (GH); Figs. 17, 18. *P. ternifolia* var. *ternifolia* with thin portions omitted: Fig. 17. Diploid, Fig. 18. Tetraploid.

that was grown in culture for several months. At Hacienda Batán, near Puebla, the tetraploids are rare, occurring in moist, shaded places while the diploids grow in exposed, rocky crevices. Other specimens, which appear to be tetraploids on the basis of the characters noted above, are quite widely distributed as is shown by the stars on the map in Fig. 7.

The cytological records of *Pellaea ternifolia* var. *Wrightiana* are based on three earlier reports from localities in the United States. Tetraploids with $n = 58$ were noted from the western part of the range in New Mexico by Lloyd (1968) and from the disjunct station in North Carolina by Wagner (1965). These plants were considered to be amphiploid hybrids of the diploids *P. ternifolia* var. *ternifolia* and *P. truncata* Goodd. (*P. longimucronata* Hook.). A triploid plant of var. *Wrightiana* with 29 bivalents and 29 univalents from Arizona was reported by Knobloch & Britton (1963). This plant was considered to have originated as a hybrid between the diploid *P. truncata* and a tetraploid plant of var. *ternifolia*. Knobloch & Britton report the same chromosome number in both mitotic and meiotic cells and also 64 irrgular spores in the sporangia. A specimen (*Pringle*, May 6) from the Santa Catalina mountains, which also appears to be a variant as noted in the survey of the spores, indicates the need for further cytological sampling of var. *Wrightiana*.

SPORES

In *Pellaea atropurpurea* only spores of the 32-spored sporangia mature, and this reduced number reflects the apogamous type of reproduction. The spores are globose or somewhat ellipsoidal (Fig. 19) and unusually large, ranging from 54-92 μ in diameter. The triradiate scar scarcely projects, and is apparent only in cleared material, with arms extending $\frac{3}{4}$ or more of the radius. The perine ridges are similar to those in *P. notabilis* but are sharper and more prominent. At higher magnification the perine surface consists of compacted sporopollenin particles (Fig. 20).

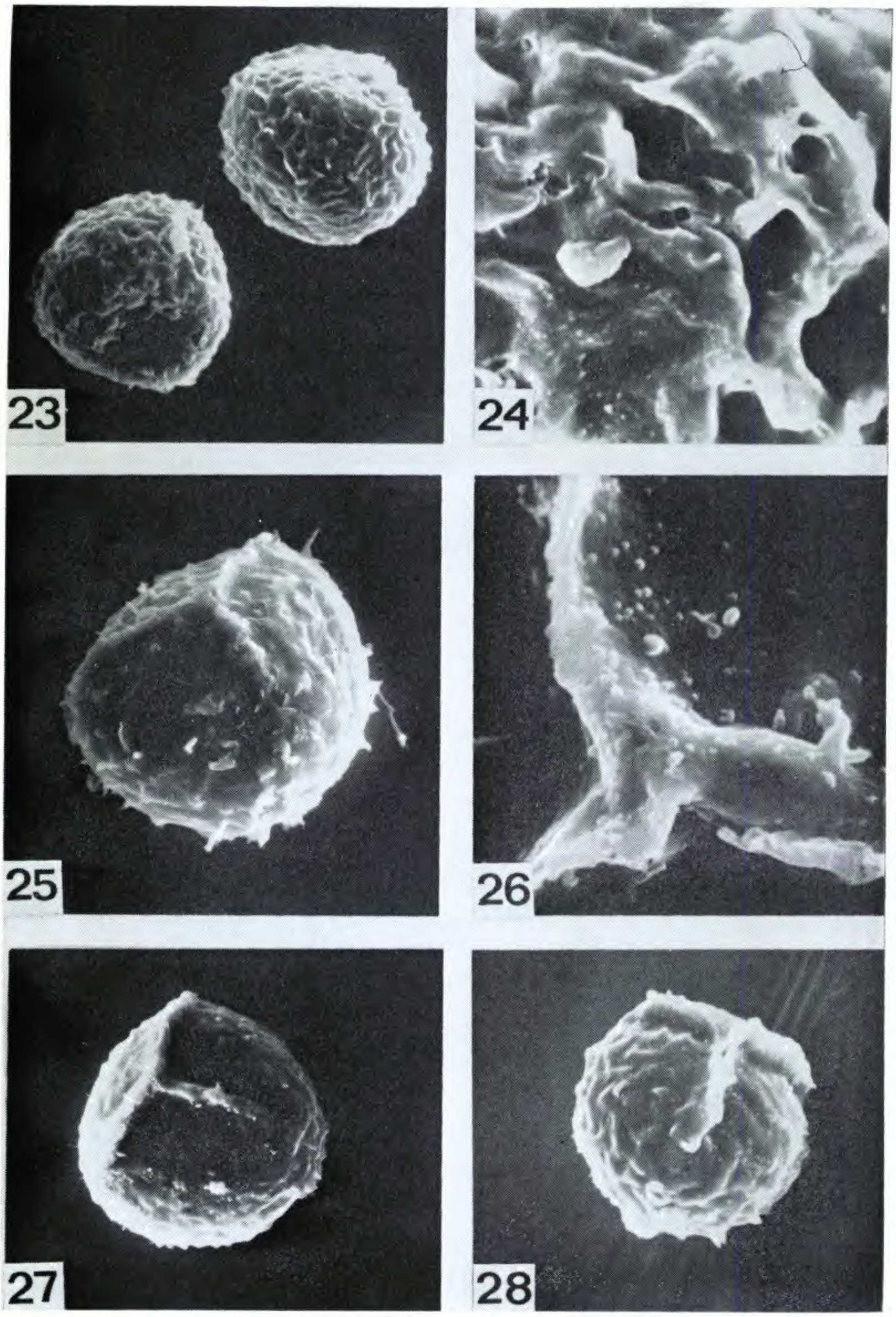


Figs. 19-22. Spores cf *Pellaea:* Figs. 19, 20. *P. atropurpurea:* Fig. 19. Nuevo Leon, *Rollins & Tryon* 5860 (GH), × 660; Fig. 20. Perine surface, Hac. Batán, *Arsène* 3548 (GH), × 3300. Figs. 21, 22. *P. notabilis:* Fig. 21. *Knobloch 1963* (GH), × 660; Fig. 22. Perine surface, × 3300.

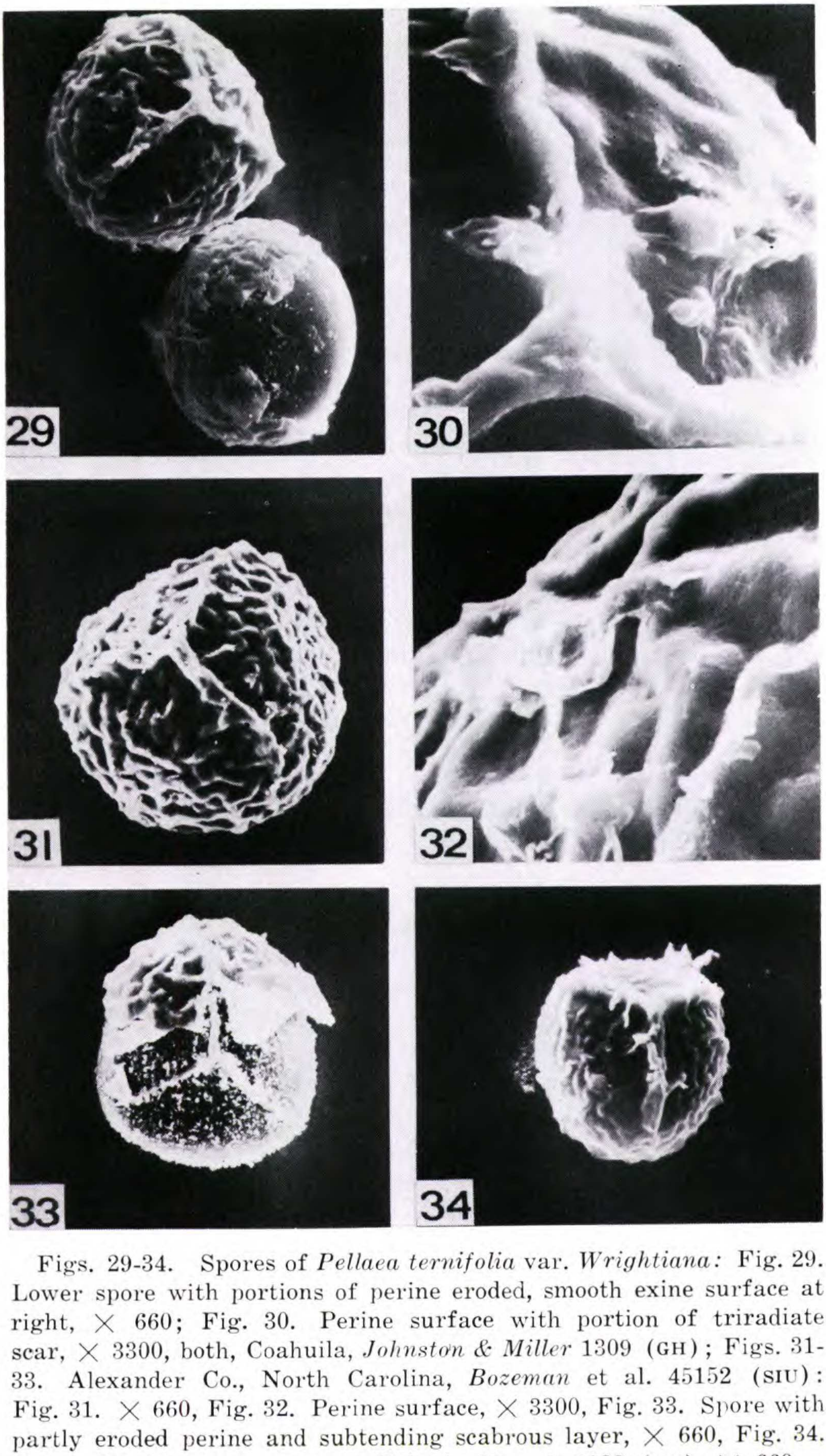
In *Pellaea notabilis* sporangia have 64 well formed spores that are globose or somewhat ellipsoidal (Fig. 21) and range from 40-62 μ in diameter. The slightly larger spore size in this diploid, relative to diploid spores in *P. ternifolia* var. *ternifolia*, may be partly due to the inclusion of the prominent ridges in the measurements. These dense ridges obscure the triradiate scar, but in cleared material it projects slightly and the arms extend ¾ of the spore radius. At higher magnification the perine deposition appears uniformly verrucate on both floor and ridge surface (Fig. 22).

In both diploid and tetraploid forms of *Pellaea ternifolia* the sporangia uniformly have 64 spores. Those of the tetraploid are consistently larger, ranging from 46-62 μ as compared to the diploids which range from 38-58 μ. The size differences are especially apparent in Figs. 23 and 25 and have been reported also in other collections by Pray (1968). Spore shape is generally spherical or tetrahedral-globose especially in the tetraploid which has broader surfaces between the arms of the triradiate scar. These arms extend ¾ or more of the spore radius. The perine is generally similar in spores of both polyploid levels, but variation occurs in density and prominence of the ridges. These may be especially prominent in the diploid spores (Fig. 24), and on the smoother surface of the tetraploid spores (Fig. 26) there are often numerous sporopollenin particles.

Spores of *Pellaea ternifolia* var. *Wrightiana* were examined from populations throughout its range. Sporangia usually have 64 spores of relatively uniform size. A specimen (Pringle, May 6, 1883, GH) collected in the Santa Catalina mountains in Arizona had many irregular spores and some small ones as shown in Fig. 34. This specimen may represent another triploid, similar to that reported from the same area by Knobloch and Britton (1963). The spores of var. *Wrightiana* are usually globose with a prominent triradiate scar extending ¾ or more of the spore radius. The form of the perine is relatively uniform as



Figs. 23-28. Spores of *Pellaea ternifolia:* Figs. 23-26. var. *ternifolia:* Fig. 23. Diploid, × 660; Fig. 24. Perine surface, × 3300, both San Luis Potosí, *Rollins & Tryon* 58219 (GH); Fig. 25. *Tetraploid,* × 660; Fig. 26. Perine surface with portion of triradiate scar, × 3300, both *Rollins & Tryon* 58218 (GH); Figs. 27, 28. var. *Wrightiana:* Fig. 27. Gillispie Co., Texas, *Correll & Correll* 12762 (GH), × 660; Fig. 28. Santa Catalina mts. Arizona, *Phillips & Reynolds* 2943 (GH), × 660.



Figs. 29-34. Spores of *Pellaea ternifolia* var. *Wrightiana:* Fig. 29. Lower spore with portions of perine eroded, smooth exine surface at right, × 660; Fig. 30. Perine surface with portion of triradiate scar, × 3300, both, Coahuila, *Johnston & Miller* 1309 (GH); Figs. 31-33. Alexander Co., North Carolina, *Bozeman* et al. 45152 (SIU): Fig. 31. × 660, Fig. 32. Perine surface, × 3300, Fig. 33. Spore with partly eroded perine and subtending scabrous layer, × 660, Fig. 34. Santa Catalina mts., Arizona *Pringle,* May 6, 1883 (GH), × 660.

shown in the series of specimens from Mexico, Arizona, Texas, and North Carolina (Figs. 27-34), although there is some variation in size and prominence of the perine. The specimens from North Carolina have an especially rugose perine with stratification as shown in Fig. 33, showing a coarse outer rugose layer subtended by a strongly scabrous one. Similar stratification is also evident in the specimen from Mexico in Fig. 29, which has some scabrous deposition on the smooth surface of the spore exine where the perine has been abraded.

The differences in prominence of the triradiate scars in these species may imply distinctions in spore development. The prominent triradiate scars with scant perine deposition characteristic of the spores of *P. ternifolia* indicate that these may have stronger tetrad associations. In contrast to these, the obscure triradiate scars in *P. notabilis* and *P. atropurpurea* suggest the tetrads may be disassociated before completion of the perine deposition.

MORPHOLOGY

Comparisons of the morphology of the species and varieties are made in Table 2. Similarities between *Pellaea notabilis* and *P. atropurpurea* (Figs. 1, 2) are especially evident in the dimorphic leaves, terete shape of the petiole, longer pinnae, and concolorous rhizome scales. These two species are readily distinguished from *P. ternifolia* by these characters. There are also marked similarities among the three kinds of *P. ternifolia* (Figs. 4-6) in the petiole shape, monomorphic leaves, and bicolorous rhizome scales. The form of the perine, in addition to the characters shown in the chart, also establishes a close relationship among them. These similarities express relationships that, by comparison to other species of *Pellaea*, can appropriately be recognized by including them in a single species.

Morphological variation in collections of *Pellaea ternifolia* var. *Wrightiana* was surveyed over the whole geographic range. Most of the specimens have leaves most closely resembling the form of the diploid var. *ternifolia* (Figs. 4, 5). Some variation is shown in the division of the leaves,

TABLE 2. MORPHOLOGICAL COMPARISONS OF THREE SPECIES OF PELLAEA

	notabilis	*atropurpurea*	*var. Wrightiana*	*ternifolia* var. *ternifolia* 2×	*var. ternifolia* 4×
Leaves	dimorphic	dimorphic	monomorphic	monomorphic	monomorphic
Lamina shape	deltoid or elongate-ovate	elongate-triangular	narrowly triangular	linear or narrowly lanceolate	linear or narrowly lanceolate
division	1 pinnate	1-3 pinnate	2 pinnate	1 pinnate	1 pinnate
Pinna length	3-7 cm.	1-12 cm.	1.0-4.5 cm.	0.5-4.0 cm.	1.7-4.0 cm.
central segment number	1	1-15	3-11	mostly 3, to 1	1-3
Petiole color	tan, atropurpureus at base	atropurpureus, rarely castaneus	castaneus	castaneus or atropurpureus	atropurpureus
shape	terete	terete or elliptical	plane on adaxial surface	plane on adaxial surface	plane on adaxial surface
indument	slightly pubescent	pubescent, hispid	glabrous or sparsely pubescent	glabrous or sparsely pubescent	lanate especially at apex
Spore size-(mean)	40-62 μ (50)	54-92 μ (64)	34-56μ (49)	38-58 μ (46)	46-62 μ (54)
Rhizome scales	concolorous, tan or rusty	concolorous, tan or rusty	bicolorous, rusty, broad central sclerotic stripe	bicolorous, tan, narrow central sclerotic stripe	bicolorous, tan, broad central sclerotic stripe

especially on the same plant, and this appears to be correlated with leaf size. In these specimens the leaves with shorter pinnae rachises and nearly ternate pinnae, resembling those of var. *ternifolia*, are usually smaller and seem to be produced before the more highly divided leaves resembling those of *P. truncata*. A similar correlation between leaf size and division is also evident in the plant from North Carolina figured by Wagner (1965). Thus, variation in leaf form in plants of var. *Wrightiana* shows types intermediate between var. *ternifolia* and *P. truncata* and also differences in developmental sequence.

DISCUSSION

The report of 29 bivalents in *Pellaea notabilis* establishes this as one of the basic species among the American pellaeas. Similarities of the spores and other morphological characters indicate that it is probably one of the elements involved in the origin of the widely distributed triploid, *P. atropurpurea*. On the basis of this new information several possibilities may be considered for the origin of *P. atropurpurea*.

The strong morphological resemblances between the two species suggest that *Pellaea atropurpurea* may be an autoploid of *P. notabilis*. The triploid could have originated from two gametes of *P. notabilis*, one of them unreduced. The studies of *P. atropurpurea* by Rigby show that affinities do exist in the two parental genomes.

However, several unique characters of *Pellaea atropurpurea* must also be considered. The broad leaves up to three times pinnate with densely pubescent rachises suggest that a second distinctive parent is involved in addition to *P. notabilis*. The cytological and morphological survey of *P. ternifolia*, the most likely parent in northern Mexico, shows that none of its variants completely fills the morphological requirements of the second parent. The spores of *P. ternifolia* are especially diagnostic, and the perine form is quite different from that of *P. atropurpurea*. The unique morphological features of *Pellaea atropurpurea* are inconsistent with an autoploid origin from *P. notabilis*, and the characters of its closest relatives near the present range of that species are inconsistent with an amphiploid origin involving one of them. The most reasonable conclusion at this time is that either the second parental element of *P. atropurpurea* belongs to another species group possibly not within the geographic center, or it may be extinct. The rare occurrence of *P. notabilis*, its closest relative in northern Mexico, suggests that the other parent may no longer be extant.

The extensive distribution of *P. atropurpurea* is undoubtedly partly based on the absence of syngamy. Elimination of the conditions required for fertilization results in more broadly adapted apogamous gametophytes. The large spores may also provide additional reserves, increased survival capacity, and a greater energy source for more rapid development of apogamous gametophytes and sporelings. In *Pellaea ovata* (Desv.) Weath., which has both a sexual ($2x$) and an apogamous ($3x$) race, the range of the latter is over 4000 miles greater than that of the sexual race. The effectiveness of the apogamous reproductive system is shown by the wider geographic distribution of the apogamous race in that species as well as in *P. atropurpurea*.

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